FURTHER OBSERVATIONS ON CHLORANTHY IN DROSERA INTERMEDIA

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(WITH PLATE XIII AND THREE FIGURES)

NAUDIN (15) was among the first to record a new method of propagation other than by seed for the genus *Drosera*. He described the appearance of buds of two young plants on the dorsal surface of a mature leaf of *Drosera intermedia*. These buds appeared between the midvein and the margins of the leaf. KIRSCHLEGER (8) made similar observations in the case of *D. capensis*. He noted buds arising from the epidermal cells at the apex or near the base of the leaf, or on the petiole itself. This species was later studied by WINKLER (19), who confirmed the observations of KIRSCHLEGER. NITSCHKE (14) described vegetative budding for *D. rotundifolia* from material collected in the field. The buds are described as appearing on the dorsal surface of the leaf, and were most commonly found in the early fall. Others have confirmed and extended the observations of NITSCHKE and the earlier data to which I have referred. GROUT (7) ascribes the appearance of these buds to excessive moisture conditions. GRAVES (6) in 1896 collected and placed plants of *D. rotundifolia* in an artificial bog. He found that a number of small plants appeared on the upper surface of old leaves, and in some cases these plants appeared from the ventral surface and edges of the leaf as in *Bryophyllum*. LEAVITT (9, 12) was able to propagate *D. filiformis*, *D. binata*, and *D. dichotoma* from cut leaves. He noticed that after placing leaves of the species named in sphagnum for a period of about 3 weeks new plants appeared from adventitious buds, which finally grew to maturity. He likewise observed that leaves, first formed from such buds in plants of *D. binata*, were orbicular like those of *D. rotundifolia;* while leaves coming from buds on *D. filiformis* were like those of *D. intermedia*. These observations, together with other studies on reversion (LEAVITT 10), led him to

the conclusion that the leaf of *D. rotundifolia* is the original type of leaf from which those of other species have arisen. AMES (1) showed the possibility of propagating *Drosera* species from old leaves cut from mature plants. He worked with *D. filiformis*, *D. intermedia americana*, *D. rotundifolia*, and *D. binata*. He noticed that when mature leaves fell on the sand in which these plants were growing, adventitious buds appeared. The condition most favorable to the development of these buds in his opinion is a low temperature.

DIXON (2), like AMES and LEAVITT, was able to obtain adventitious buds on leaves of *D. rotundifolia*. He differs with GROUT in that he asserts that adventitious buds appear only when the parent plant is allowed to dry out. He found that under these conditions the leaves of *D. rotundifolia* produce adventitious buds on the dorsal surfaces after 2 months. He also found that new plants may arise in the axils of leaves and between the petiole and main axis of the inflorescence as axillary buds. GOEBEL (4) showed further that a portion of a leaf of *D. binata* could produce adventitious buds. He cut an arm of a leaf of *D. binata* and placed it on a moist substratum. After a time he observed the appearance of adventitious buds whose leaves were rounded and similar to those of *D. rotundifolia*, and he states that these leaves agree in shape with those of the young plants of *D. binata*.

Miss ROBINSON (17) repeated the work of LEAVITT, AMES, and GOEBEL, with similar results. She describes the appearance of roots on the young adventitious buds which appeared on leaves of *D. rotundifolia* placed in sphagnum. She also found that leaves placed with the dorsal surface down developed buds on the upper or ventral surface. Miss ROBINSON holds that these adventitious buds are in no way connected with the vascular system of the parent plant.

SALISBURY (18) found the appearance of adventitious buds in *D. rotundifolia* and *D. intermedia* Hayne. Signs of these buds appear on the leaves of these 2 plants in the late spring of the year following their removal to the greenhouse. The age of the leaf which bears these buds may vary. The first leaf rudiment appears as a small protuberance on the dorsal surface of the leaf. This is

followed by another leaf rudiment opposite the first, and the next leaves follow in succession, forming a rosette-like structure in the axils of the leaves first formed. As against Miss ROBINSON, KIRSCHLEGER and WINKLER, SALISBURY maintains that sections through these buds show that they are connected with the fibro-vascular bundle of the leaf on which they appear. Salisbury believes that these buds form a definite reproductive mechanism in these species of plants.

GOEBEL (5) reports on *D. pygmaea* the appearance of a highly specialized type of brood body resembling in shape the gemmae of *Marchantia*. These bodies appear in rosettes and are dorsi-ventral. The under surface of each body is smooth, while the upper surface is horseshoe-shaped. Stomata and vascular bundles are present. GOEBEL believes that each brood body arises from a leaf *anlage*.

PLANCHON (16) described an anomaly in the flowers of *D. intermedia*. He asserts that the ovary becomes elongated and the carpels bear both tentacles and ovules. All gradations between an ovule and a tentacle were found. The petals of these flowers were likewise modified, being leaflike in nature and bearing tentacles. PLANCHON asserts that all organs become chloranthic except the calyx. FERNALD (3), while collecting bog plants, found a form of *D. rotundifolia* in which the inflorescence was subcapitate and consisted of a few flowers. The petals and sepals were greenish to crimson in color, and the ovary instead of producing a normal capsule formed a rosette of glandular foliage leaves. This tendency was noted in other floral organs. LEAVITT (11) studied these flowers and states that they are quite sterile. FERNALD makes no mention of stamens. It seems that they are generally absent, and this constitutes the main difference between this form and the one described later. The constancy of this abnormality in *D. rotundifolia* led FERNALD to make a new variety which he called *D. rotundifolia comosa*. Neither FERNALD nor LEAVITT gives figures of these modified flowers. FERNALD regards them as a means of vegetative propagation.

In studying the development of pollen my attention was attracted by the appearance of a number of plants of *D. intermedia*.

These were growing in the water, and at the apex of the flower stalk a head of tentaculiferous flowers was borne. Again, in August 1915 I found in the same locality a number of these plants. They were growing in the water of a shallow arm of Horicon Lake, Lakehurst, New Jersey. The plants were of the long-stemmed type such as has been figured by NITSCHKE (14) for *D. rotundifolia*, and extended about 4–5 in. above the surface of the water. Associated with them was a *Castalia* species, and the banks of the bog were covered with sphagnum in which *D. rotundifolia* and *D. filiformis* grew in great abundance. Normal plants of *D. intermedia* were present also. These abnormal inflorescences resemble in all respects those described by FERNALD (3) for *D. rotundifolia*. The plants were not so numerous; in fact, the monstrosity appeared in comparatively few plants. As the case is quite a striking one, I have thought it worth while to figure and describe the abnormal flowers in some detail. Herbarium specimens have been deposited in the New York Botanical Garden.

The plants bearing the abnormal flowers were in all other respects like the normal *D. intermedia*. Under the conditions in which they were growing the exposed leaves and their tentacles were reddish. The long stem and delicate roots were submerged and buried in the mud. The apical portion of the stem bears an imperfect rosette of leaves. Here also appears the short, thick flower stalk on the summit of which the abnormal heads of greenish flowers are found. On superficial examination (text figs. 1–3), the small headlike inflorescences seem to be mere clusters of diminutive leaves. More careful study shows that the cluster is really a group of chloranthic flowers. The term "chloranthy," as used here, indicates that all or nearly all of the organs of the flower assume the appearance and form of leaves (13). Each flower is commonly subtended by 3 bracts. These bracts are narrow, lanceolate, leaflike structures which may have small sessile glands. All the parts of the flower except the stamens have become leaflike. This is a more extreme case of chloranthy than that described by PLANCHON (16). The chloranthic flowers of an inflorescence are in different stages of development, the size of the flower generally indicating its relative age. The largest I found

were 6–8 mm. in diameter, and the smallest were 1–2 mm. in diameter. There is no correspondence between the degree of development of the flower and its position in the inflorescence. They seem to be promiscuously scattered over the slightly thickened end of the flower stalk.

There are 5 sepals as in the normal flowers. They are slightly green and have a number of tentacles as shown in fig. 2. The marginal tentacles are generally larger and as a rule vary in number

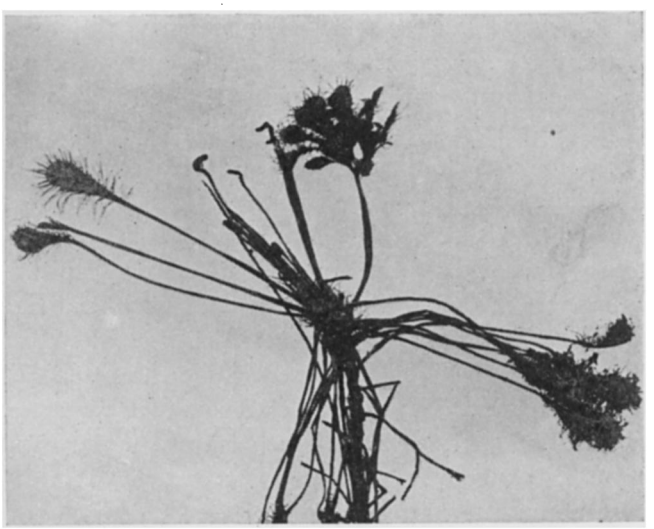

FIG. 1

from 2 to 4. The surface tentacles have smaller stalks and are very often lacking. In one case I found 2 adjacent fused sepals as shown in fig. 1, which represents the ventral surface of the calyx showing the attachment of the sepals. The tentaculiferous petals alternate with the sepals. While in the normal flower they are usually white or pinkish in color, in the chloranthic flowers they are pale green, and, as noted, covered with a varying number of normal tentacles (fig. 3). The shape of these petals is like that of the foliage leaf with the characteristic spatulate blade and a rather long, narrow, and flattened petiole. The tentacles are scattered quite regularly along the margin and over the surface

of the blade. The marginal ones are larger. Inside this whorl of petals there are 5 stamens. These appear to be in every respect normal and compare favorably in size and shape with the stamens in normal flowers. Normal tetrad pollen grains have been found in their anthers (fig. 4). In the case (fig. 5) of one flower which is mentioned later, the filaments were broader and the anthers in some cases consisted of a single locule each, yet all intermediate stages between unilocular and bilocular anthers were present. In these anthers no pollen was found. Unlike PLANCHON'S (16) chloranthic flowers of *D. intermedia*, these had no carpels or any indication of carpels (figs. 6, 13). The center of the flower was occupied by a cluster of leaf rudiments in various stages of development, as described by FERNALD (3) and LEAVITT (11) for *D. rotundifolia* leaf. The outer leaf rudiments are best developed, while the ones toward the center are progressively smaller (fig. 6). In older flowers these rudiments have become fully developed spatulate blades resembling those of the normal vegetative leaf. In a single capitate inflorescence all stages in the development of the central leaf rudiments can be found. Fig. 7 represents a small chloranthic flower in such a head. The sepals are fully developed, while the petals, although they are fully expanded, have not all extended their tentacles. The unfolding leaflike petals show the characteristic incurved form common to the vegetative leaves. The stamens in this flower (fig. 7) are normal and are few in number. The carpels as such are entirely lacking, but are replaced by a small number of very minute leaf rudiments, of which one is considerably larger than the others. Figs. 8 and 9 represent larger chloranthic flowers. The sepals shown in fig. 8 are larger and much broader than the average I observed. In the center of the flower there is a large rosette of young leaves entirely replacing the carpels (fig. 8). The outer leaf rudiments are large and almost ready to unfold. Fig. 9 represents a chloranthic flower in which the leaves are slightly farther advanced. Fig. 10 represents a chloranthic flower in which the central leaves have attained the greatest development I found. The flower measured approximately 6 mm. in diameter. Only one petal and sepal are figured, but the usual number 5 was present here also. The outer whorl of the apical leaf group has fully

developed into 4 comparatively large spatulate leaves covered with numerous tentacles and having a well developed vascular system (compare modified sepals, petals, and leaves in fig. 10). The central rosette of young leaves is large and in all appearances resembles the normal winter buds common to *D. intermedia*.

The cases figured represent what appears to be the ordinary structure of the chloranthic flowers in this species of *Drosera*, but variations from this type can be found. Fig. 11 represents a

FIG. 2

flower in which some of the leaves in the petal series have few tentacles. Fig. 12 represents one of a cluster of 6 flowers in a capitate inflorescence in which an abnormality appeared. In this flower the number of sepals is reduced to 2; they have tentacles and are like those previously described. The number of petals is likewise reduced. The stamens are 5 in number and are characterized by having broad filaments (fig. 5) with anthers, as just noted, consisting of 1 or 2 locules in which no pollen grains were found. The leaf rudiments resemble those in the ordinary chloranthic flowers. Although I have not observed their further development, there can be no doubt that these chloranthic flowers serve as a

means of vegetative propagation. The central rosette of leaf rudiments is comparable to a diminutive form of winter bud, such as is common to this and other species of the *Drosera*. The appearance of tentacles and especially chlorophyll on the petals of the chloranthic flowers may be an adaptive feature to enable the flower to maintain itself until rooted in the substratum.

FERNALD'S (3) monstrous flowers in *D. rotundifolia comosa* appear to be the most marked case of chloranthy described for the

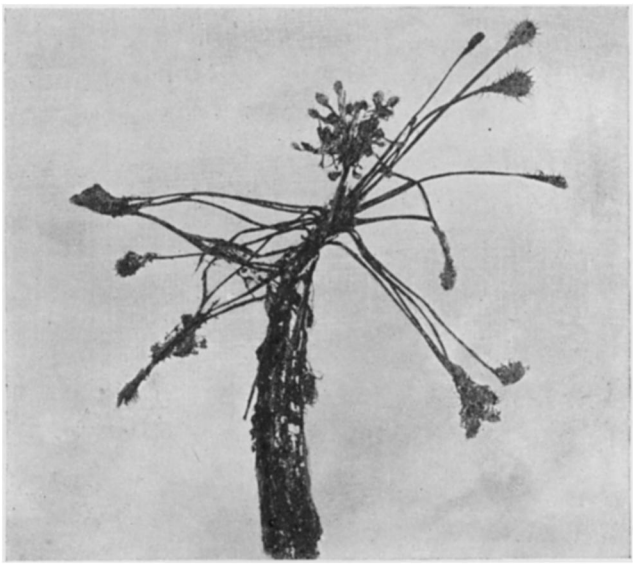

FIG. 3

genus. The organs of the flowers of this species may all become modified and assume the appearance of leaflike structures. It seems that vegetative propagation is absolutely essential to the perpetuation of this form. PLANCHON'S case of chloranthy in *D. intermedia* shows flowers with organs least modified. The calyx in these flowers never becomes modified and the normal carpels may also be present. The stamens and the petals are invariably modified. In the case observed all the organs except the stamens are modified to assume the form of tentaculiferous leaves. The carpels are replaced by a rosette of leaves resembling

a winter bud. The degree of chloranthy is more developed than in the case described by PLANCHON, and appears also to be more constant, although abnormalities among the monstrosities occur. It appears from these cases that the degree of chloranthy may vary. It may be argued that a case like the one described in the present paper is less abnormal than the other cases mentioned. It appears that normal pollen may be formed, and under favorable conditions cross-pollination may take place between these forms and the normal species of *Drosera;* that is, sexual reproduction has not entirely disappeared. At the same time, these plants appear to be capable of propagating themselves vegetatively by the chloranthic flowers which may function as buds. The case is perhaps parallel to the adventitious buds on the leaves.

The conditions which favor the development of these flowers are not evident. It may be, as suggested by GROUT for adventitious buds, that an abundance of moisture is very essential. It seems from FERNALD'S observations and my own that chloranthic flowers in *Drosera* species are formed only in plants which grow in water. The bearing of such cases of reversion of flowers to vegetative buds on our general conception as to the relation of sexual and asexual reproduction is not very clear. It appears, however, that under unfavorable conditions vegetative reproduction replaces in part, if not altogether, the sexual method. This is contrary to our general conception of reproduction, since it is commonly conceded that under favorable conditions vegetative reproduction prevails almost entirely to the exclusion of sexual reproduction.

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EXPLANATION OF PLATE XIII

All figures were drawn with the aid of a Leitz hand lens ocular 10.

CHLORANTHIC FLOWERS OF DROSERA INTERMEDIA HAYNE

FIG. 1.—Ventral surface of a calyx of a chloranthic flower in which 2 sepals have fused.

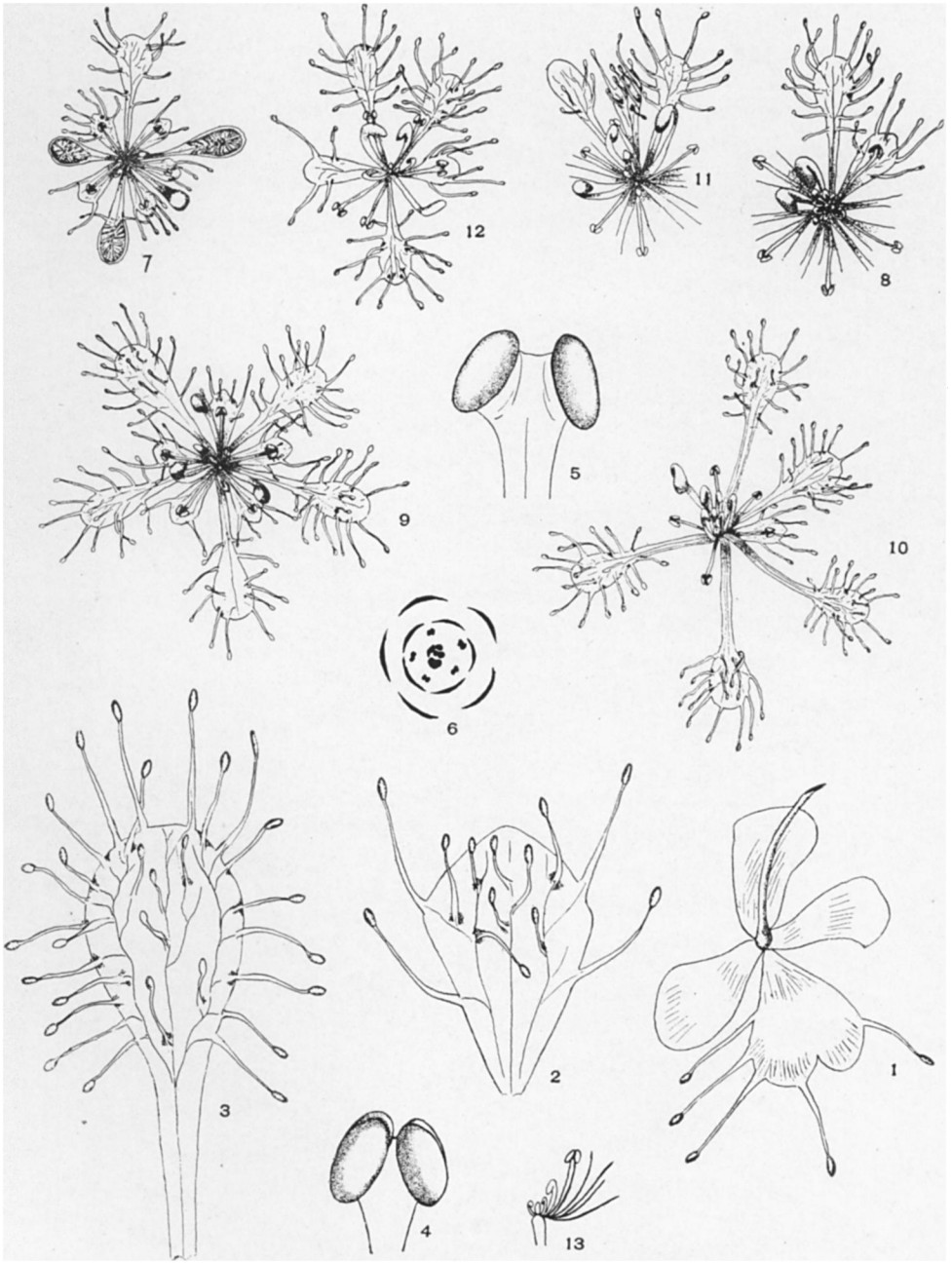
FIG. 2.—Dorsal surface of a sepal of a chloranthic flower covered with tentacles.

FIG. 3.—Dorsal surface of a petal of a chloranthic flower showing numerous tentacles.

FIG. 4.—Normal stamen of a chloranthic flower in which normal pollen is borne.

FIG. 5.—Abnormal stamen in which no pollen is found.

FIG. 6.—Schematized cross-section of chloranthic flower.



LEVINE on CHLORANTHY

FIG. 7.—Young chloranthic flower in which the leaflike petals are not yet fully developed; the carpel is replaced by a number of leaf rudiments.

FIG. 8.—A slightly older stage; sepals very large.

FIG. 9.—Another slightly older stage.

FIG. 10.—An older stage in which outer whorl of leaf rudiments are developed into leaflike organs resembling normal spatulate leaf of *D. intermedia*.

FIG. 11.—Variation of a chloranthic flower in which the number of tentacles on the petals is relatively small.

FIG. 12.—Another abnormal chloranthic flower in which the number of sepals and petals is reduced to 2 and 3 respectively and the stamens are abnormal, as in fig. 5.

FIG. 13.—Schematized longitudinal section of a chloranthic flower.